Letters

Kin recognition by self-referent phenotype matching in plants

When plants of *Arabidopsis thaliana* are cultivated in rows of coetaneous kin neighbours (plants of the same accession) the growth of their leaves is horizontally reoriented towards the empty spaces out of the row, increasing self-shading and reducing mutual shading among plants (Fig. 1a). This growth pattern is not observed among nonkin plants (plants of a different accession) or noncoetaneous plants. The leaf-position response requires similar body shapes and hence vertical light profiles perceived by neighbours, a requisite not fulfilled by nonkin plants (Fig. 1c). Based on these observations Crepy & Casal (2015) concluded that plants are able to recognize kin neighbours by the matching of their body shapes (phenotype matching). In their Letter, Till-Bottraud & de Villemereuil (2016; in this issue of *New Phytologist*, pp. 13–14) question whether this is actually a case of 'kin recognition or phenotype matching'.

In order to address this issue it is important to consider the definition of kin recognition. A simple definition of kin recognition is 'the ability to discriminate between related and unrelated individuals' (Mehlis *et al.*, 2008). In *A. thaliana*, leaf position responds differentially to kin (Fig. 1 in Crepy & Casal, 2015), that is, plants discriminate between kin and nonkin; therefore one is forced to conclude that plants are able to recognize their kin. Differential plant responses to kin involving root (Mahall & Callaway, 1991; Dudley & File, 2007) or volatile (Karban *et al.*, 2013) signals have also been reported. According to Mateo (2004), 'kin recognition is an internal process of assessing genetic relatedness that can be inferred through kin discrimination, the observable differential treatment of conspecifics based on cues that correlate with relatedness'. Similarly, according to Holmes (2004), kin recognition is the 'ability to distinguish kin vs nonkin using genetic similarity or any cues that are correlated with kinship'. These conditions are met in the case of *A. thaliana*. First, there is kin discrimination (differential response). Second, there is correlation of the cue with relatedness because the aboveground body shape of the plant (leaf shape and size and rosette structure) is more similar within the same accession (genotype) than among accessions (Pérez-Pérez *et al.*, 2002). Third, there is an 'internal' process which requires signal perception and transduction, as evidenced by the failure of specific mutants (Fig. 1b). Penn & Frommen (2010) explicitly exclude restrictions to the application of the term kin recognition based on the mechanism or evolutionary functions. They argue that strict definitions have added little to our understanding and would be more suitable as hypotheses about the underlying mechanisms. They also cite the opinion of Hamilton that 'it seems on the whole preferable to retain a more flexible use of terms'.

The use of stringent definitions of kin recognition has implications that do not apply when the term is used in its most simple meaning. The occurrence of kin recognition defined as the ability to discriminate by genetic similarity, does not allow to conclude, without further analysis, that individuals of this species have evolved to distinguish kin from nonkin, or that possession of the ability has anything to do with kin selection (Grafen, 1990). For animals, kin recognition can be important for territory establishment and defence, dominance hierarchies, reciprocal altruism, mate choice, parent–offspring interactions and nepotistic contexts, among several other possibilities (Mateo, 2004). Following the terminology of West *et al.* (2007), Crepy & Casal (2015) conclude that in *A. thaliana* kin recognition leads to mutual benefit, that is, a response that is beneficial to both the actor and the recipient, and does not lead to altruism, because the response is not costly to the actor and beneficial to the recipient on the basis of the lifetime direct fitness consequences. Therefore, Crepy & Casal (2015) do not discuss their results in a context 'in which altruism might be selected for as long as it is directed toward kin' as suggested by Till-Bottraud & de Villemereuil (2016).

Four not mutually exclusive mechanisms of kin recognition are often acknowledged in the literature. Kin recognition can be based on spatial distribution, familiarity or association, phenotype matching, and/or recognition alleles (Blaustein, 1983; Mateo, 2004). Since in the case of *A. thaliana* kin recognition depends on the similarity of body shapes and light profiles, the mechanism can be assimilated to phenotype matching (Crepy & Casal, 2015). Furthermore, taking into account that kin recognition occurs when the template of the neighbour is similar to the body shape of the own plant that assesses the light profile to respond (Fig. 1), the mechanism could be defined as self-referent phenotype matching (Mateo, 2004). Of course, the definitions based on the animal literature do not perfectly fit to the case of plants. In animals, phenotype matching requires learning the cues from siblings or parents, and self-referent phenotype matching requires learning their own cues. No learning would be required in plants.

As noted by Till-Bottraud & de Villemereuil (2016), a green vertical filter elicited a response similar to that elicited to a kin neighbour without involving a kin (Fig. 5 in Crepy & Casal, 2015). This experimental protocol was designed (after several failures) to provide a strong signal from one side at leaf height without shading the leaf from above. These two features would be characteristic of the light profile of kin but not of that of nonkin neighbours. Till-Bottraud & de Villemereuil (2016) argue that 'a formal proof of kin recognition would be to show that the response is sensitive not only to shape but also to kinship, for example, that plants of similar shape but genetically unrelated do not show the leaf-position response'. However, the model proposed by Crepy & Casal (2015), actually predicts that if a plant is sufficiently similar in body shape it should be taken as kin, even if that were not the case because as a

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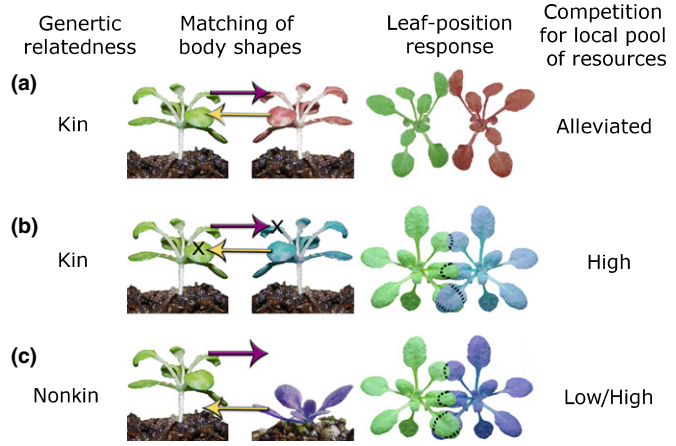

Fig. 1 The horizontal leaf-position response requires phenotype matching, which is more likely among kin neighbours, and alleviates mutual shading among plants. (a) Kin neighbours, (b) kin neighbours unable to perceive or to respond to the signal, (c) nonkin neighbours. Matching of body shapes: the arrows represent light signals produced by a plant, which may reach or not reach the receptive foliage of the neighbour. X indicates a mutation that impairs perception or transduction of the light signal and therefore abolishes the leaf-position response. Leaf-position response: the border of the leaf area that becomes shaded by the neighbour is indicated by a dotted line. Plants represented in false colours.

downstream step in the mechanism, similar body shapes would bypass the need of kinship. It is clear that the response should be measured in different ecological contexts to quantify the probability of finding unrelated plants of sufficiently similar shape to elicit the leaf-position response.

Till-Bottraud & de Villemereuil (2016) argue that phenotype matching could serve to assess competitive ability rather than to assess kinship. The interpretation proposed by Crepy & Casal (2015) is that the leaf-position response on a horizontal plane helps to alleviate the strong competition for light that would otherwise be established among kin that place their foliage at a similar height. The primary selective force for this behaviour would be the benefit associated to the reduced mutual shading (Fig. 1). This response pattern can therefore be regarded as a way to assess competitive ability. However, while doing so, the plant discriminates kin from nonkin neighbours and therefore there is kin recognition. In other words, in this context, kinship would be linked to both the potential of enhanced competition for local pools of resources and to the ability to change leaf position on the horizontal plane and alleviate competition for local resources (Fig. 1).

In summary, the main difference between the concepts expressed by Till-Bottraud & de Villemereuil (2016) and Crepy & Casal (2015) is in the use of the term kin recognition. We understand that the availability of mutants among other tools in the plant field offer the option to test independently different aspects of the whole process (e.g. the mechanisms of kin recognition, the evolutionary significance of kin recognition) (Fig. 1b). These approaches are only beginning to be used and much remains to be done. In our opinion, in this scenario it would be better to keep the simplest meaning of the term kin recognition.

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